

SOME OBSERVATIONS ON THE INTERNAL
ANATOMY OF *DIGUETIA CANITIES* (MCCOOK, 1890)
(ARANEAE, DIGUETTIDAE)

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ABSTRACT

Diguetia canities (and probably other Diguettidae species also) is mainly characterized by the massive development of the poison glands, a double rostral organ, a large U-shaped coxal labyrinth, a deep prosomatic pigmentation, a group III epigastric glands, four kinds of silk glands and a new opisthosomatic structure: the supra-anal organ. These character states support Gertsch's (1958) idea linking the family with Plectreuridae between the Dysderoidea and Scytodoidea.

INTRODUCTION

The family Diguettidae is a small group of haplogyne spiders established by Gertsch (1949). It comprises only one genus, *Diguetia* Simon 1895, with about eight species (Gertsch 1958), all being restricted to America (the southwestern United States and Mexico).

The Diguettidae are cribellate Araneomorphae considered to be primitive, owing to certain characteristics of their genital anatomy, in particular the rather unspecialized epigynum and the simple copulatory bulb with an expansive spatulate conductor.

According to Gertsch (1949), the Diguettidae should be included in the section Plecturoidea, together with Plectreuridae, these two families seeming closely related by virtue of their geographical distribution, ocular area and genitalia structure. Gertsch (1958) furthermore assigns an intermediate status to Plectreuridae between the Scytodoidea and Dysderoidea. Brignoli (1978), on the other hand, integrates the Diguettidae into the Scytodoidea. The geographical distribution, biotopes and spinning-work of Diguettidae were originally studied by Gertsch (1935, 1949, 1958). Cazier and Mortenson (1962) later detailed the sheet-space composite web, the retreat ("cocoon") and feeding habits of *Diguetia canities* (McCook 1890). Lastly, prey capture and silk handling were examined thoroughly by Eberhard (1967) in *Diguetia albolineata* O. P. Cambr. However, except for a brief description of the vulva and its adnexa (Gertsch 1958), no study of internal anatomy has been performed, to my knowledge, in Diguettidae. This is why I intend to expose the main results of a general histological study of *Diguetia canities* (McCook 1890) in the present paper, thus filling the gap, describing new spider structures and attempting to establish some relationships between internal anatomy and phylogeny.

MATERIAL AND METHODS

I collected the specimens of *D. canities* (3 males, 4 females and 1 immature) in southwestern Utah, near Zion National Park, alongside the primary state road n° 15 (August 1981). In this semi-arid area, the spiders were established on *Opuntia* ("chollas" and "prickly pears" cactus), a favorite site for Diguettidae (Gertsch 1949, 1958; Cazier and Mortenson 1962).

After preservation in alcoholic Bouin's fluid, the *Diguettia* were later embedded in cytoparaffin and serially sectioned. The sections (6 μm thick) were colored by routine staining techniques: Gabe and Martoja's triple coloration, Masson-Goldner, Groat's hematoxylin-eosin-orange G.

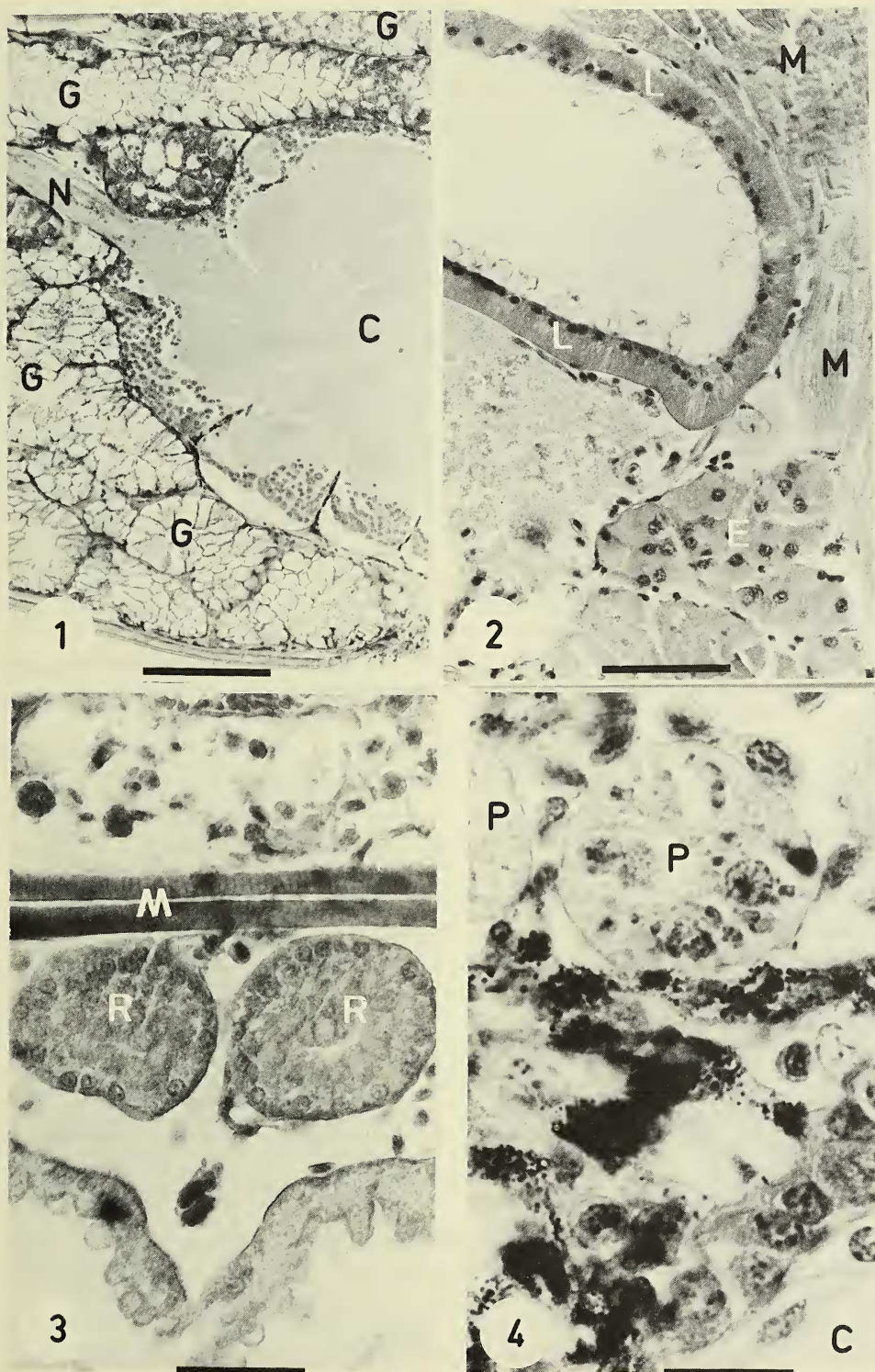
RESULTS

In the prosoma the venom glands, the coxal glands, the rostral organ, the endocrine tissue, and the male palpal bulbs were examined; pigment cells deeply located were discovered on this occasion. In the opisthosoma, the study was directed to genitalia, the male epigastric glands, the silk apparatus and the supra-anal area, which includes a new type of organ.

Venom gland.—The venom gland is remarkable for its large size, a particularly striking character of this species. The gland takes up, at least one half of the prosoma where it encloses a large part of the nervous system (Fig. 1). Ramifying in many directions the gland's pocketlike diverticula extend into the rostrum, run down along the pharynx, its so-called "taste organ" and stretch back to the cauda equina, between the suboesophageal ganglia and sternal epidermis. Except for its intracheliceral part, the gland wall, 30 μm thick, is evenly formed in all parts by a connective sheet, a basement membrane and an inner folded secretory epithelium that surrounds a rather narrow lumen. Tall columnar prismatic glandular cells show dark staining basal nuclei and clear cytoplasm containing a small amount of a coarse granular acidophilic secretion. Muscle fibers cannot be identified beneath the basement membrane. In contrast, the intracheliceral part of the venom gland is characterized by a broader lumen and a cuboidal epithelium, just above the short venom duct. Its cells are filled with a uniformly granular acidophilic secretion.

Coxal glands.—The system of coxal glands is extremely well developed in *D. canities*. Each of the two glands includes a small sacculus facing the first leg, a conspicuous labyrinth and a short chitin-lined exit tubule, devoid of a "bladder." The labyrinth, curved into a U-shape tube, shows a prominent anterior concavity. It is formed by two, sinuous, coupled, roughly parallel limbs, one external, running backward from the sacculus, and one internal, running forward to the exit tubule. Both are mainly visible in cross sections of the prosoma. The wide lumen of each limb is bordered with an acidophilic epithelium 20 μm high showing the usual striated cellular bases on which large clear nuclei rest (Fig. 2).

Rostral organ.—The rostral organ appears, as in other spiders, as an epidermal invagination of the anterior face of the rostrum. However, it is not a single recess but a double pocket, composed of two blind parallel tubes (Fig. 3). Moreover, the wall is devoid of the usual striated cuticular component. It is reduced to an epithelium 25 μm thick with tall foamy cytoplasm, basal round nuclei and convex apices. The rostral cuticle remains at a distance, without invaginating into the cavities, and appears to "float" above their anterior opening.



Figs. 1-4.—*Diguettia canities*, prosoma: 1, poison gland; 2, Labyrinth of coxal gland; 3, rostral organ (cross section); 4, pigmentary cells. Abbreviations: C, cerebrum; E, endocrine tissue; G, gland; L, labyrinth; M, muscle; N, nerve; P, nephrocyte; R, rostral organ. Scale lines for Figs. 1 = 80 μ m; 2 = 60 μ m; 3 = 25 μ m; 4 = 15 μ m.

Endocrine tissue.—The endocrine tissue (Millot 1930a) or “moulting gland” (Bonaric 1980) is well represented in *Diguetia* but only located in the prosoma. It appears as numerous ribbon-like or trabecular aggregations of small polymorphous cells, provided with an acidophilic cytoplasm and a vesicular nucleus (Fig. 2). These cellular islets are distributed, some laterally against the muscle and coxal glands, above the pedipalp and leg nerves, the others along the cauda equina. All associate with large nephrocytes, the cytoplasm of which includes pigmentary grains (Fig. 4).

Pigment.—This pigment, dark purplish-brown in color, is seen again in the cavities of the endochondrites, the walls of vessels and, chiefly, in the cells of the neurilemma. The latter are loaded with grains filling their poorly limited cytoplasm and concealing their clear nuclei (Fig. 4); they lie around the appendicular nerves, the cerebral mass, the suboesophageal ganglia, inclusive metameral partitions, and the cauda equina.

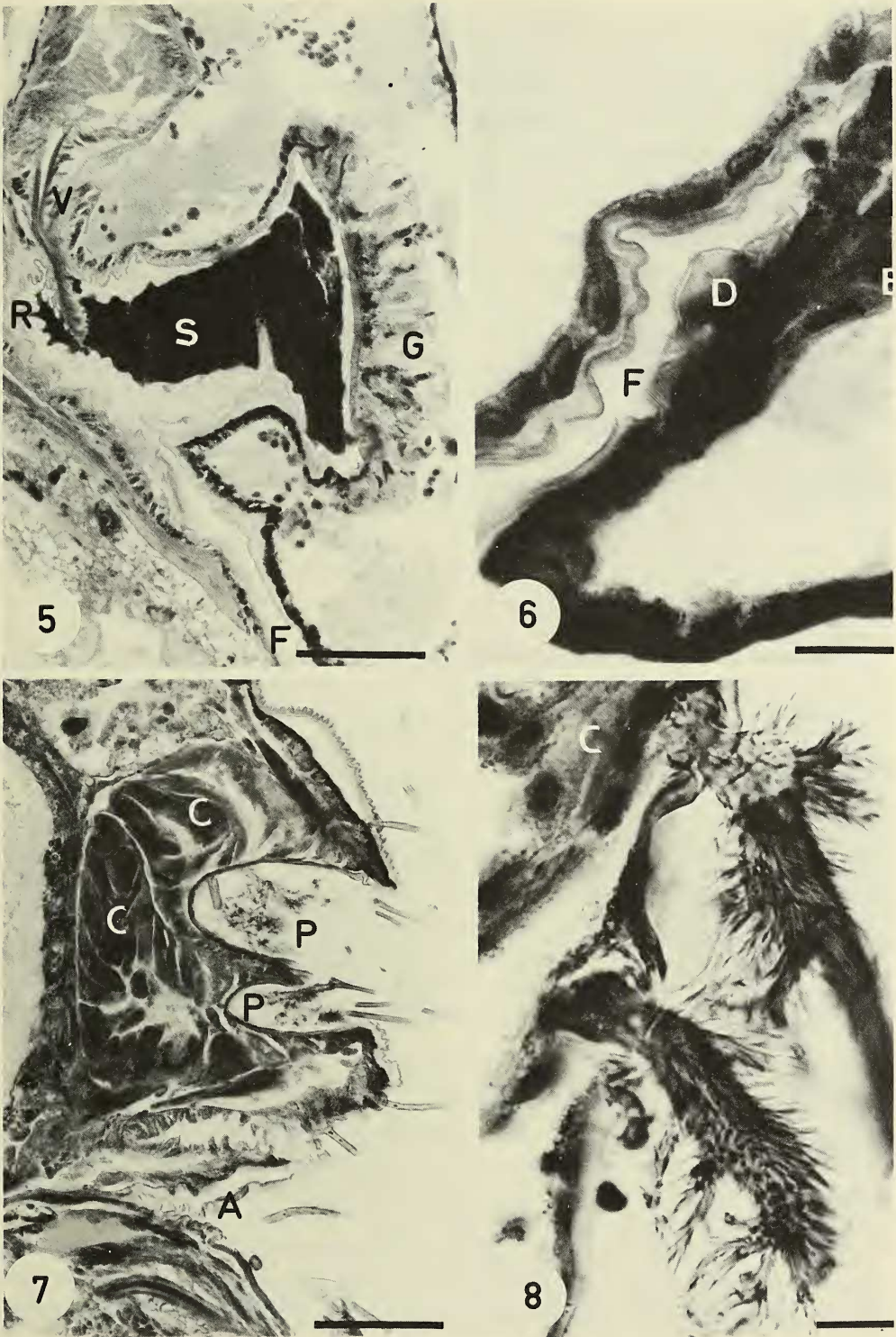
Male palpal bulb.—It includes a receptaculum seminis showing a wide lumen and a rather simple parietal structure. The fenestrate part of its cuticular wall delimits a spacious “outer palpal room” together with an adjoining basophilic secretory epithelium, the festoons of which delimit some recesses.

Female genitalia.—The female genitalia display, in the sagittal sections of their outer part all the details already outlined by Gertsch (1958:8, Fig. 17). The bursa copulatrix is wide and characterized by the presence of special glandular cells lying ventrally under its wall cuticle (Fig. 5). These cells are slender elements, 30 μm high, arranged in convex lobules and showing a clear “combed” cytoplasm. Their separate excretory ductuli are presumably bordered with microvilli, then with duct cells and abut on tiny cups of the above-lying cuticle. Such glandular cells are lacking in the seminal receptacle, the wall of which is reduced to a cuticle and to an endotheliform flat epithelium.

Male genital tract.—This includes two long sinuous tubular testes, displaying a classical spermatogenesis, and a pair of much coiled vasa deferentia which unite at their extremities just before terminating at the epigastric furrow. The sperm cells filling the lumina are encysted individually; they do not cluster into “spermatolophids”. The anterior lip of the epigastric furrow appears devoid of the pregonoporal acinuous epigastric glands described by Lopez (1974). On the contrary, this lip includes the gonoporal type of such organs, composed of several separate unicellular glands. Each of them is provided with a tiny excretory ductulus which opens into the furrow: after crossing the pigmented epidermis, it pierces the cuticle through a small nipple-like thickening (Fig. 6).

Supra-anal organ.—The supra-anal area is singularized by the presence of an unusual organ occurring in adults of both sexes, as well as in immature specimen. Four pocket-like tegumentary invaginations, about 120 μm deep, open just above the anal orifice. Their modified cuticle bears ramose spiny hairs distinct from the neighbouring serrate ones. Several clusters of large chromatic cells lie beneath this cuticle. They are provided with conspicuous nuclei and gather into bag-shaped formations, apparently connected with the bases of the hairs (Figs. 7, 8).

Silk apparatus.—It comprises various glands that can be placed in four categories, according to their situation and cytological patterns and are enumerated from anterior to posterior. Category A is represented by ventral ovoid acini with short excretory ducts joining anterior spinnerets, scalloped lumen and large epithelial cells. Only belonging to one type, the latter show conspicuous nuclei and spongy basophilic cytoplasm. Category B glands are the two largest components of the silk apparatus. Their long looping ducts also open onto the anterior spinnerets. In their bodies, an ampulla and a long coiled tube can be identified; they seem to be composed of three kinds of adenocytes: one proximal,



Figs. 5-8.—*Diguertia canities*, opisthosoma: 5, female genitalia; 6, one epigastric gland; 7, supra-anal area; 8, hairs of supra-anal organ. Abbreviations: A, anus; C, cell cluster; D, ductulus near termination; E, G, gland cells; F, epigastric furrow; P, pit; R, receptaculum; S, semen; V, vaginal valve. Scale lines for Figs. 5, 7 = 60 μ m; 6, 8 = 15 μ m.

with a fine basophilic secretion; one intermediate, with a foamy cytoplasm; one distal, characterized by its plentiful spherule secretion and huge irregular nucleus. Category C glands lie between the rectum and the category B glands, and abut on the median spinnerets. They include acidophilic distal cells and intensely basophilic proximal cells, which together produce a bilayered secretion. Category D glands are also bipartite. Atrophied in the male, they show a proximal segment, with dark secretion grains, and a distal one, with clear acidophilic secretion and numerous superimposed pigmentary grains. The ducts are connected to the posterior spinnerets.

DISCUSSION

The unusual organ of the supra-anal area has apparently not been observed in any other spider. Whether it is peculiar to *Diguetia* or exists in other spiders is a question for future research. Owing to the cellular cluster connections with special ornamented hairs and the absence of evident excretory ducts piercing the cuticle of the pits, a parallel can be drawn, with the "tubes cellulaires non sécréteurs" (Millot 1931 d) or "glandes tubulaires" (Kovoor 1980) described in the basal part of *Uroctea* anal tubercle. However, the new organ of *Diguetia* is located above the anal tubercle; an integumentary fold separates it from the anal opening. In the absence of data on its fine structure, the precise function, sensorial, glandular or both, cannot yet be determined.

The occurrence of deep intracellular pigmentation is an infrequent feature, fortuitously discovered by a histological review. The single outstanding instance known elsewhere is provided by a pholcid, *Holocnemus pluchei* Scop., the pigment of which is carried by stellate cells, includes the opisthosoma and thus appears more widespread (Legendre and Lopez 1973). It is not yet possible to credit the pigment either with an active part in *Diguetia* physiology or to consider it as a superfluous metabolic waste.

The massive development of the poison glands is the most striking anatomical characteristic in *D. canities*. A similar massive venom apparatus was described previously in two other spiders: *Filistata insidiatrix* (Forsk.) (Millot 1931 a, 1949) and *Plectreurys tristis* Simon (Millot 1935). This last species displays a multilobed ramified pattern of its poison glands which similarly fill the greatest part of the cephalothorax. It also seems that *Ero aphana* (Walck.), a mimetid, possesses huge venom glands (Kovoor, pers. com.). The wide neck and its special epithelium strongly resemble the differentiations noticed in Dysderidae, Sicariidae, Palpimanidae and Pholcidae (Millot 1931 a), at least in histological sections. Given their extensiveness, the venom glands of *D. canities* probably deliver a profuse secretion, perhaps enriched with and strengthened by a product secreted by the neck. The high potency which might result from such a large volume may explain why preliminary wrapping is not required and only used to prevent loss during subsequent attacks (Eberhard 1967). An analogous correlation of extensive venom glands with an overwhelming, predominantly biting attack can be established in Filistatidae and Mimetidae (Berland 1922, Gertsch 1949, Bristowe 1958).

The coxal glands, another conspicuous anatomical feature in *D. Diguetia*, resemble strongly, by their labyrinth, the condition established as primitive by Buxton (1913) in Dysderidae and Sicariidae. They therefore become an integral part of group II, created by this author for the two other families.

The division of a rostral organ into two wholly separated blind bags has not been previously described in Araneae, although a slight bilobate pattern was noticed in various araneid species. Thus-shaped during the post-embryonic life of *Diguetia*, the double rostral organ is most interesting from the ontogenic standpoint because it appears as a

partial preservation and thus new evidence of the rostrum paired anlagen. The latter were formerly suggested by studies of nervous system development (Legendre 1959) and the discovery of cephalic coxal glands in the adults of some spider species: *Leptoneta microphthalmma* and *Metepeira incrassata* (Lopez 1978).

The endocrine tissue or "moulting gland" of *D. canities* shows a condition distinct from that noticed in primitive Araneomorphae: in the Filistatidae and Sicariidae, it is said to be non-existent, and in the Dysderidae it seems to be quantitatively reduced, in a very lateral position (Millot 1930a). On the other hand, in its abundance (more than its location) it resembles the condition in the Pholcidae.

The male genital apparatus is in conformity with the general scheme of those spiders which do not produce spermatophores. The spermatozoa are not packed into "spermatolophids" and consequently differ from the sperm cells of Dysderidae because, in the latter family, a characteristic "spherulation" occurs (Lopez 1972). The palpal bulb has an elementary histological structure somewhat resembling that of Mygalomorphae and haplogyne Araneomorphae.

The gonoporal-type epigastric glands terminate in extended order; they can be related to a new intermediate stage, that could occupy special position between group II (Dysderidae) and group IV (Pholcidae) of my original epigastric gland classification (Lopez 1974). Their secretion is probably added to the spermweb prior to induction.

The female genitalia show, in sagittal section (Fig. 5) a structure schematized by Gertsch (1958). Taking into account position and histological features, the ventral cells annexed to the bursa copulatrix can be interpreted as tiny glands that produce a sex pheromone, possibly mixed with the sperm as in other spiders (Kovoor 1982). By their strictly anteroventral location, the specialized cells of female *D. canities* differ from the dorsal cells of Pholcidae, but resemble the anterior cells of Dysderidae.

The silk apparatus shows a relatively small number of its glands. However, it tends to resemble that of more highly evolved and efficient spinners in its overall volume, as pointed out by Kovoor (1977) in Pholcidae. The complexity and size of the web that is built by *Diguetia* can thus be explained, as well as the cocoon-industry (Cazier and Mortenson 1962); on the other hand, the reduction of prey wrapping is inconsistent with the volume of the silk glands and seems to parallel, as already mentioned, poison apparatus development. It is noteworthy that some cytological features of silk producing epithelium (large size of cytoplasm and nuclei, deep basophilia of certain secretions) are also encountered in the Scytodidae, Segestriidae, Dysderidae and, mainly in Pholcidae (Millot 1929, 1930^b, 1931^{b,c}).

As a result of this study, it appears that the internal anatomy of *D. canities* and probably that of the rest of the genus, displays a puzzling mix of characteristics that expresses various evolutive degrees. Some of them are undoubtedly primitive (male receptacula seminis, coxal glands, female genitalia, double rostral organ). Others seem to be more derived (endocrine tissue, silk apparatus). The evolutionary stages represented by the venom glands and the supra-anal organ are unknown. The venom gland and the female genitalia unquestionably link Diguettidae closely with Plectreuridae. Unfortunately, we know little about the other plectreurid character states, and cannot now see how extensive this linkage may be. The Diguettidae, also resemble the Filistatidae (venom glands), Scytodidae (coxal glands, silk glands), Pholcidae (venom glands, endocrine tissue, silk glands), Dysderidae and Segestriidae (silk glands, neck of venom gland, coxal and epigastric glands). Hence it follows that the family Diguettidae cannot be rigidly included in Scytodoidea; it now appears more rational to follow Gertsch's opinions (1949, 1958) which linked them with the Plectreuridae, between the Scytodoidea and Dysderoidea.

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LITERATURE CITED

- Berland, I. 1922. Contributions à l'étude de la biologie des Arachnides. (1er mémoire). Ann. Soc. ent. France, 91:193-208.
- Bonarcic, J. C. 1980. Contribution à l'Etude de la Biologie du développement de l'Araignée *Pisaura mirabilis* (Clerck, 1758). These Doct. es. Sci. Univ. Montpellier II.
- Brignoli, P. M. 1978. Some Remarks on the Relationship between the Haplogynae, the Semientelegynae and the Cribellatae (Araneae). Symp. Zool. Soc. London, 42:285-292.
- Bristowe, W. S. 1958. The World of Spiders. Collins, London, 304 pp.
- Buxton, B. H. 1913. Coxal glands of the Arachnids. Zool. Jahrb., 14:231-282.
- Cazier, M. A. and M. A. Mortenson. 1962. Analysis of the habitat, web design, cocoon and egg sacs of the tube weaving spider *Diguetia canities* (McCook). Bull. Soc. California. Acad. Sci., 61:65-88.
- Eberhard, W. 1967. Attack behavior of *Diguetia* spiders and the origin of prey wrapping in spiders. Psyche, 74:173-181.
- Gertsch, W. J. 1935. Spiders from the Southwestern United States, with Descriptions of new Species. Amer. Mus. Novitates, N° 792, 31 pp.
- Gertsch, W. J. W. 1949. American Spiders. D. Van Nostrand, Toronto, New York, London, 285 pp.
- Gertsch, W. J. 1958. The Spider Family Diguetidae, Amer. Mus. Novitates, n° 1904, 24 pp.
- Kovoor, J. 1977. La soie et les glandes séricigènes des Arachnides. Ann. Biol., 16:97-171.
- Kovoor, J. 1980. Données nouvelles sur le tubercule anal d'*Uroctea durandi* (Latreille) (Araneae: Oecobiidae). Proc. 8th Intern. Cong. Arachn., Vienna (Jul. 7-12 1980): 297-302.
- Kovoor, J. 1982. Une source probable de phéromones sexuelles: les glandes tégumentaires de la région génitale des femelles d'Araignées. C. R. VIe Coll. Arachnol. expr. fr., Modena-Pisa (28 Août-1 Sept. 1981): 1-15.
- Legendre, R. 1959. Contribution à l'étude du système nerveux des Araneides. Ann. Sci. nat. Zool. Biol. an., 1:339-473.
- Legendre, R. et A. Lopez. 1973. Les chromatophores de l'Araignée *Holocnemus pluchei* (Scop.) (Pholcidae). Note préliminaire. Bull. Soc. zool. France, 98:487-494.
- Lopez, A. 1972. Morphologie et rapports particuliers des glandes épigastriques dans deux familles d'Araneides: Les Dysderidae et les Clubionidae. (Note préliminaire). Bull. Soc. zool. France, 97:113-119.
- Lopez, A. 1974. Glandes épigastriques et classification des Araneides. Bull. Assos. Anat., 58:899-904.
- Lopez, A. 1978. Présence de glandes coxales céphaliques chez les Aranéomorphes. C. R. Acad. Sci. Paris, 286:407-409.
- McCook, H. C. 1890. American Spiders and their Spinning Work, 2:135-136.
- Millot, J. 1929. Les glandes séricigènes des Pholcides. Bull. Soc. zool. France, 54:194-206.
- Millot, J. 1930^a. Le tissu réticulé du céphalothorax des Araneides et ses dérivés: néphrocytes et cellules endocrines. Arach. Anat. micr., 26:43-81.
- Millot, J. 1930^b. Glandes venimeuses et glandes séricigènes chez les Sicariides. Bull. Soc. zool. France, 55:150-175.
- Millot, J. 1931^a. Les glandes venimeuses des Araneides. Ann. Sci. nat. zool., 14:113-147.
- Millot, J. 1931^b. Les glandes séricigènes des Dysdérides. Arch. zool. exp. gén., 71:38-45.
- Millot, J. 1931^c. Les glandes séricigènes des Pholcides (2ème article). Bull. Soc. zool. France, 56: 75-83.
- Millot, J. 1931^d. Le tubercule anal des Urocteides et des Oecobiides (Araneidae). Bull. Soc. zool. France, 56:199-205.
- Millot, J. 1935. La glande venimeuse de *Plectreurys tristis* Sim. (Araneides). Bull. Soc. zool. France, 60:460-462.
- Millot, J. 1949. Ordre des Araneides. In P. P. Grassé, Traité de Zoologie. Masson, Paris, 6:589-743.
- Simon, E. 1895. Sur les Arachnides recueillis en Basse-Californie par M. Diguët. Bull. Mus. Hist. nat., 1895:105-107.